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Title: Historic and prehistoric human-driven extinctions have reshaped global mammal diversity patterns

Authors: S. Faurby[1$*], J-C. Svenning[1]

Affiliations:

[1] Section for Ecoinformatics & Biodiversity, Department of Bioscience, Aarhus University, Ny Munkegade 114, DK-8000 Aarhus C, Denmark

$ Current address: Department of Biogeography and Global Change, Museo Nacional de Ciencias Naturales, CSIC, Calle José Gutiérrez Abascal 2, Madrid 28006, Spain

*Correspondence to: faurby@mncn.csic.es

Running title:

Humans have reshaped mammalian diversity patterns.

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Abstract:

Aim: To assess the extent to which humans have reshaped Earth's biodiversity, by estimating natural ranges of all late Quaternary mammalian species, and to compare diversity patterns based on these with diversity patterns based on current distributions.

Location: Globally

Methods: We estimated species, functional and phylogenetic diversity patterns based on natural ranges of all mammalian species (n=5747 species) as they could have been today in the complete absence of human influence through time. Following this we compared macroecological analyses of current and natural diversity patterns to assess if human-induced range changes bias for evolutionary and ecological analyses based on current diversity patterns.

Results: We find that current diversity patterns have been drastically modified by humans, mostly due to global extinctions and regional to local extirpations. Current and natural diversities exhibit marked deviations virtually everywhere outside sub-Saharan Africa. These differences are strongest for terrestrial megafauna, but also important for all mammals combined. The human-induced changes led to biases in estimates of environmental diversity drivers, especially for terrestrial megafauna, but also for all mammals combined.

Main conclusions: Our results show that fundamental diversity patterns have been reshaped by human-driven extinctions and extirpations, highlighting humans as a major

force in the Earth system. We thereby emphasize that estimating natural distributions and diversities is important to improve our understanding of the evolutionary and ecologically drivers of diversity as well as for providing a benchmark for conservation.

Keywords

Extinction, functional diversity, macroecology, mammals, megafauna, phylogenetic diversity

(A). Introduction

Human activities increasingly affect the whole Earth system (Crutzen, 2002), driving an ongoing global mass extinction (Barnosky *et al.*, 2011), massive environmental changes (IPCC, 2013), and a looming planetary biosphere state shift (Barnosky *et al.*, 2011). A largely overlooked consequence of these anthropogenic transformations is that they also influence our ability to understand the factors that have generated and maintained Earth's biodiversity, one of the most important questions for contemporary science (Pennisi, 2005). Mammals represent one of the most studied organism groups, and the general distribution of most mammalian groups is well known (Schipper *et al*., 2008). This knowledge has been used to study patterns in species, functional, or phylogenetic diversity (Safi *et al*., 1011; Huang *et al*., 1012; Jetz & Fine, 2012; Mazel *et al*., 2014), as well as conservation (Sodhi *et al*., 2010). However, mammals are also one of the clades most influenced by human activities, such as habitat loss (Schipper *et al*., 2008; Spear & Chown, 2008; Sandom *et al*., 2014). Therefore, it is not clear to what extent current diversity patterns, or estimates of drivers of these, reflect natural patterns or are biased by anthropogenic modifications

Human activities have strongly influenced the distributions of many mammalian species during the last few millenia through range contractions (Short & Smith, 1994; Laliberte & Ripple 2004), extinctions, (notably on islands (Turvey & Fritz, 2011)), and to a lesser extent introductions of species now considered native (Bover & Alcover, 2008). Furthermore, accumulating evidence indicates that humans have been a major driver of

severe Late Pleistocene and early Holocene large-mammal extinctions (Burney & Flannery 2005; Sandom *et al*., 2014). This raises the question of how diversity patterns would look today without any human modifications of species distributions, i.e., given the present-natural ranges *sensu* Peterken (1977) for all late Quaternary mammals. The term "present-natural" refers to the state that a phenomenon would be today in the absence of human influence; for simplicity, we hereafter refer to this concept by the term 'natural'. We see this as a technical term unrelated to discussions of whether humans should be considered within or seperate from nature.

The majority of on diversity patterns in mammals make predictions about natural diversity patterns, but test them on current diversity patterns (e.g. Sandom *et al.*, 2013). The potential problems of this have previously been pointed out (Blackburn & Gaston, 1998). Yet, no previous study has systematically estimated the natural distribution of all species within larger clades, and empirical studies have been forced to ignore this issue, even though this may confound conclusions from studies of natural drivers. The goal of this paper is to estimate natural diversity patterns of mammals (i.e., without anthropogenic effects) . This is not just crucial for diversity studies, but also essential for conservation, notably for providing base-lines for restoration efforts (Donlan *et al.*, 2005).

No single diversity measure fully captures all biologically relevant elements of diversity (Devictor *et al.*, 2010); therefore, we estimated natural patterns not just for taxonomic diversity (species richness), but also for phylogenetic and functional diversity. The use of

multiple diversity measures is especially interesting because all previous analyses of prehistoric faunal losses have focused solely on taxonomic richness (Johnson, 2002; Sandom *et al*., 2014). We also analyzed the effects of human-induced changes in diversity on the relationships between diversity and key environmental factors to investigate if analyses of current diversity patterns may be biased. We expect the largest differences for larger animals because both the Late Pleistocene extinctions and the later range contractions have been size selective (Koch & Barnosky, 2006; Ripple *et al*., 2014). We also expect geographic variation in the difference between current and natural diversity due to variation in human impact (De Thoisy *et al*., 2010), and a higher sensitivity of island or island-like faunas (Duncan *et al*., 2013; Sandom *et al*., 2014). Furthermore, some habitat types may have higher sensitivity than others, with large, dense forests and steep mountains being less vulnerable (Johnson, 2002) and desert regions being more vulnerable (Yeakel, 2014).

(A) Materials and methods

(B) Range modifications

We used the taxonomy of Faurby & Svenning (2015) for this study. We did not include potential Late Pleistocene species if no certain Late Pleistocene or Holocene records could be found and therefore discarded some relatively well-known species such as *Bubalus mephistopheles* and *Eulamaops paralellus*. A full list of the considered but omited continental species we considered, but where we could not find such dates can be

found in Table S1 of Sandom *et al.* (2014), while most of the island species discussed by Turvey & Fritz (2011), but not included by us likewise miss such dates. For all species, we attempted to estimate their potential current natural ranges (Peterken, 1977). Climatic data were used to estimate this range for some species, but we only aimed to identify the areas that would be inhabited without human interference, not the entire possible potential range based on the estimated niche. Therefore, dispersal constraints, biotic constraints, and non-climatic abiotic limiting factors were also taken into account when estimating natural ranges. We systematically inspected the IUCN ranges (Schipper *et al*., 2008) of all species suspected to have had anthropogenically-induced range changes based on red-list category (vulnerable, endangered, critically endangered, extinct, extinct in the wild, or data deficient: 2302 species), body size (larger than 1 kg: 627 additional species), or occurrence in large isolated island-like systems (Australia, New Guinea, or Madagascar: 340 additional species). These ranges were modified when evidence for anthropogenic range changes was found. The remaining species were not systematically investigated, but their ranges were modified whenever we found evidence for human-caused range changes. We modified the ranges of 1085 species, though for 85 of them the range modifications were too small to affect our analyses at our chosen grid size (110 × 110 km). A total of 260 species were not accpted by IUCN but by us because they went extinct prior to 1500 AD, but within the last 130,000 years. We note that both longer periods than 130,000 years as in Rhodin *et al.* (2015) or shorter periods e.g.based on likely arrival date of humans in Australia could be used instead. We chose 130,000 because it includes the Eemian, which is the last period with similar climate to present,

and because most of the species with last appearance date between 130,000 and 40,000 years are poorly known and may have survived substantially longer than the last record (Brook *et al.*, 2013). There are very few species from the Late Pleistocene with well-documented extinctions prior to human arrival.Most species clearly survived until close to human arrival or beyond (e.g., Dantas *et al.*2013), although the giant Caribbean rodent *Amblyrhiza inundata* (Biknevicus *et al*., 1993) may represent such a pre-human arrival extinction. We implicitly assumed that all global and continental extinctions during this period were caused by humans rather than natural phenomena, such as climatic variations, due to the overwhelming evidence for strong human involvement in most of these extinctions (Turvey & Fritz 2011; Sandom *et al*., 2014), but did allow for natural regional extinctions due to climate changes, e.g., the disappearance of *Ovibos moschatus*, *Gulo gulo* and other cold-adapted species from Southern Europe after the end of the ice-age (Álvarez-Lao & García, 2010).

Overall, the modifications led to a change from a total of 1,983,482 to 2,212,446 occurrences in 110 × 110 km cells (1,073,129 to 1,298,365 occurrences for non-marine mammals and 67,306 to 242,960 occurrences for megafauna). A detailed explanation of the modifications can be found in supplementary methods.

(B) Estimated diversity

All diversities were estimated on a equal-area Behrman projection of the world with 360 columns (i.e., 1° by 1° cells at the equator, roughly equal to 110 × 110 km grid cells).

Diversities were estimated for five mammalian subgroups: 1) *all species*, 2) *non-marine species*, 3) *terrestrial species*, 4) *large terrestrial species*, and 5) *terrestrial megafauna*. For *non-marine species*, species coded as exclusively marine by IUCN (most cetaceans and two manatees), as well as pinnipeds coded as "marine and terrestrial" and three effectively marine non-pinniped carnivores (*Ursus maritimus*, *Enhydra lutris* and *Lontra felina*), were removed, whereas species coded as "freshwater and marine", such as *Phoca vitulina* or manatees of the genus *Trichechus*, were deleted from all fully or partially marine cells. For *terrestrial species* all manatees, cetaceans, pinnipeds, and bats were removed from *non-marine species* (whereas mainly freshwater species fully capable of land movement such as *Ornithorhynchus anatinus* or *Castor* sp. were kept). This list was further restricted in *large terrestrial species* to species larger than 10 kg, the definition of megafauna used by Sandom *et al*. (2014), and in *terrestrial megafauna* to species greater than 44.5 kg, the classical definition of megafauna used by many studies (Barnosky *et al*., 2004).

Analyses were performed on species, phylogenetic, and functional diversity. The phylogenetic diversity of each cell was defined as the median tree length of the species in the cell based on 100 trees from the posterior distribution of the phylogeny (Faurby & Svenning, 2015). Our treatment of functional diversity is a multidimensional version of the bin-filling approach of (Huang *et al*., 2012). For the functional diversity analyses of *all species* and *non-marine species*, we used three dimensions of niche space, habitat, body size, and diet, whereas the analysis of the three terrestrial subsets only focused on body size and diet (see supplementary methods).

Three diversities were estimated for each cell: 1) current diversity, 2) natural diversity of historically extant species, and 3) total natural diversity. *Current diversity* was the diversity following IUCN, excluding species ranges coded as introduced and species ranges coded as extinct or possibly extinct (5). *Natural diversity of historically extant species* was the natural diversity of all species accepted by IUCN (species ranges coded as extinct or possibly extinct by IUCN, as well as our modified ranges of species accepted by IUCN, were included, but species that went globally extinct prior to 1500 AD were not). Furthermore, for species that went continentally extinct (considering Eurasia as one continent) prior to 1500 AD, the natural distributions on these continents were removed. Therefore *Equus ferus* in North America, South America, and Africa, *Camelus dromedarius* in Africa and Eurasia, *Cuon alpinus* and *Saiga tatarica* in North America, *Bos primigenius* in Africa, and *Crocuta crocuta*, *Hippopotamus amphibius*, *Macaca sylvanus,* and *Ovibos moschatus* in Eurasia were removed. *Total natural diversity* included the full natural distribution of all species whether accepted by IUCN or not. We focus on the differences between *current diversity* and *total natural diversity*, and refer to *total natural diversity* simply as *natural diversity* throughout the main article. Separate maps showing the patterns for *Natural diversity of historically extant species* are shown in the supplementary figures.

We also estimated the total deficit (the difference between *current diversity* and *total natural diversity* divided by the *total natural diversity*), the historic loss (the difference between *current diversity* and *natural diversity of historically extant species* divided by the *total natural diversity*), and the prehistoric loss (the difference between the *natural*

194 *diversity of historically extant species* and the *total natural diversity* divided by the *total*
195 *natural diversity*). These terms are defined temporally, but a limited temporal overlap
196 between the two exists. For example, the massive prehistoric loss in the Caribbean
197 mainly occurred within the middle to late Holocene (Steadman *et al*., 2005), whereas
198 most of the range contractions of *Panthera pardus* in Europe occurred earlier (Sommer &
199 Benecke, 2006). For some species the loss in range was a slow and gradual process,
200 exemplified by *Equus ferus*. The decline in this species started near the end of the last
201 ice-age with continental extinctions in the Americas (Haile *et al*., 2009), whereas the last
202 wild specimen in Europe died in the 19th century (Nowak, 1999) and the last wild
203 specimen globally died in the 20th century (Schipper *et al*., 2008).

204

205 **(B) Statistical analysis of diversity**

206 We analyzed geographic variation in diversity for 45 different analyses: all combinations
207 of the three diversities (species, phylogenetic, and functional), five datasets (terrestrial
208 megafauna, large terrestrial mammals, all terrestrial mammals, non-marine mammals,
209 and all mammals) and current, IUCN natural, and total natural diversity. Our analysis had
210 nine variables (seven main effects and two interactions). These were: 1) elevation range,
211 2) annual temperature (Hijmans *et al*., 2005), 3) logarithm transformed annual
212 precipitation (Hijmans *et al*., 2005), 4) precipitation seasonality (Hijmans *et al*., 2005), 5)
213 temperature seasonality (Hijmans *et al*., 2005), 6) NDVI (Tucker *et al*., 2005), and 7)
214 "open areas" (a binary indicator variable separating all non-forest cells (areas with

Tropical and Subtropical Grasslands, Savannas and Shrublands, Temperate Grasslands, Savannas and Shrublands, Flooded Grasslands and Savannas, Montane Grasslands and Shrublands, Tundra, or Deserts and Xeric Shrublands (Olson, 2001)) from forest cells (Tropical and Subtropical Moist Broadleaf Forests, Tropical and Subtropical Dry Broadleaf Forests, Tropical and Subtropical Coniferous Forests, Temperate Broadleaf and Mixed Forests, Temperate Coniferous Forest, Boreal Forests/Taiga, Mediterranean Forests, Woodlands and Scrubs, or Mangroves (Olson, 2001)). This measure scores estimated pre-clearing vegetation type, but we cannot guarentee correct scoring of natural conditions in all cases especially if the disapperence of the mega-fauna caused shifts between non-forest and forest biomes). The interactions were: 8) annual temperature and open areas and 9) annual temperature and annual precipitation. All parameters except "open areas" were standardized to have a mean of 0 and a standard deviation of 1. The interactions and the last parameter were intended to take into account that diversity may be different in forest and non-forest biomes, especially for megafauna because such species may not have access to the plant resources in the canopy. The six first parameters were similar to ones used in earlier analyses to estimate the role of various hypotheses behind diversity gradients (e.g., Currie *et al*., 2004; Safi *et al*.,2011). They were not chosen to evaluate the relative roles of the various proposed mechanisms, but to estimate the magnitude of the potential bias in macroecological analyses solely relying on current distributions.

To remove spatial autocorrelation in the data, we analyzed the data based on the SAR_{err} model (Simulaneous Auto-Regression assuming spatial error), (Kissling & Carl, 2008).

SAR models are computing intensive; therefore, we chose to perform them using cells equivalent to 4° squares at the equator. We tried neighborhoods for each SAR model of between 1 and 8 neighbors and selected the best model based on AIC. Next, we estimated the overall model performance by calculating the square of the correlation between the predicted (only the predictor, not the spatial parts) and raw values. We refer to this as pseudo-R^2 throughout the paper even though this term is ocationally used for other test-statistics as well (UCLA: Statistical Consulting Group, 2014). To make comparisons between different models easier, we kept all parameters in the models, even if they were not significant and used the neighborhoods in the SAR analyses that minimized the AIC for the corresponding *total natural diversity* for c*urrent diversity* and *natural diversity of historically extant species*.

(A) Results

(B) Diversity gradients

We focus on the patterns for all terrestrial species (n = 4465) and terrestrial megafauna (n = 330). Three other datasets (large terrestrial species ≥10 kg (n=570) with results similar to those for megafauna; non-marine species (n= 5635), and all species (n=5747) with results overall similar to all terrestrial species) are reported in the appendix (Fig S1-S10). The differences between current and natural diversities were substantially larger for megafauna than for all terrestrial species (Fig. 1). The changes in species, phylogenetic and functional diversity were similar.

258

259 **(B) Geographic variation in diversity decifits**

260 Geographic patterns in the difference between current and natural diversity (hereafter
261 referred to as deficits) in species, phylogenetic and functional diversity exhibit similar
262 geographic patterns (Fig. 2). The largest deficits in megafauna diversity occur on islands
263 (Madagascar, Caribbean, Oceania) and the island-like continent Australia (Fig. 2). Strong
264 deficits are also found in the Americas and Greater Sahara, whereas deficits are only
265 minor in Africa and tropical Asia and intermediate in the remaining regions. The
266 temporal patterns of the losses behind these deficits are radically different. Some regions,
267 such as Australia, New Guinea and the Caribbean islands, and the Americas, had almost
268 exclusively prehistoric losses, others had mainly historic losses, such as Greater Sahara
269 and Africa, whereas still other regions - most noticeably Europe –had both large historic
270 and prehistoric losses. In all regions, the relative deficits for all terrestrial species are
271 substantially smaller than the megafauna losses.

272

273 **(B) Biases in the inference in diversity drivers**

274 The substantial and geographically variable anthropogenic diversity deficits could have
275 large effects on our ability to understand macroscale diversity patterns. We therefore
276 compared the results of parallel standard macroecological analyses of current and natural
277 diversity patterns and found that the explanatory power (pseudo-R^2) was consistently

lower for current diversity than for natural diversity for all studied mammalian groups. Furthermore, the models for natural diversity based only on historically extant species consistently had intermediate pseudo-R^2 values between the two (Tables S1-S3). The decreases in pseudo-R^2 were especially large for terrestrial megafauna (approximately 0.2 for all three diversity measures). The higher explanatory power for the natural diversity is noteworthy given that these are known with less certainty than the current diversity, and these uncertainties would be expected to reduce the pseudo-R^2 values.

Two other consistent changes were seen in analyses of current vs. natural diversity. In all analyses, the normalized difference vegetation index (NDVI), an indicator of vegetation productivity (Wang *et al*., 2004), was the strongest predictor of diversity, with higher diversity in areas with higher NDVI, but its predictive power was always lower for current diversity than for natural diversity. Elevation range was a weaker, but consistent, predictor (with higher diversity with higher elevation range), but with a consistently stronger effect on current diversity divided by natural diversity. The changes in pseudo-R^2, NDVI, and elevation range were strikingly regular, with a larger change in pseudo-R^2 also corresponding to a larger change in the effect sizes of NDVI and elevation range (Fig. 3).

(A) Discussion

(B) Diversity gradients

298 For terrestrial megafauna, the pattern in natural species diversity is radically different
299 from the current pattern (Fig. 1A and B). Current species diversity exhibits a well-known
300 peak in Sub-Saharan Africa, whereas Africa's natural species diversity is similar to other
301 continents, as suggested previously (Owen-Smith, 2013). For natural diversity, the
302 highest values are observed in the southern Rocky Mountains, Mexico and northern
303 Argentina, whereas most of the Americas and Eurasia have diversities similar to the most
304 diverse areas in sub-Saharan Africa (Fig. 1A and B). Differences between current and
305 natural diversities for all terrestrial species are smaller than for megafauna, with the
306 largest changes occurring on islands (including Australia) and some temperate areas in
307 Europe and North America (Fig. 1C and D). The patterns in phylogenetic diversity are
308 similar to the patterns in species diversity (Fig. 1E-H versus Fig. 1A-D), except that
309 natural phylogenetic diversity is elevated in the Americas relative to Africa and Southeast
310 Asia, reflecting greater diversity at deep phylogenetic levels in South America, as seen by
311 tabulating the number of mammalian orders containing terrestrial megafauna.

312 The natural and current megafauna in Africa belong to six orders, whereas the natural
313 megafauna diversity in South America belongs to nine, only five of which have extant
314 megafauna species in South America. The high natural phylogenetic diversity of the New
315 World may be owing to the former isolation of South America, followed by the effects of
316 the Great American Biotic Interchange (GABI) (Simpson, 1980). Even though many of
317 the formerly endemic South American mammalian groups went extinct due to
318 competition with invading Northern Hemisphere clades, several survived until the Late
319 Pleistocene or early Holocene (Barnosky *et al*., 2004; Sandom *et al*., 2014). However, the

320 species diversity within many of these clades was low during the Late Pleistocene, with
321 only a few species from the formerly diverse clades (Billet, 2011), creating a pattern of
322 long branches and high phylogenetic diversity. The GABI could potentially also
323 influence species diversity. As already suggested by Darwin (1859), related species may
324 compete more, and two areas of equal productivity may potentially support more species
325 if they are distantly related. The evidence for this is limited (Cahill *et al*., 2008), but a
326 functional coupling between the high megafauna ordinal diversity in the Americas and
327 the region's very high natural megafauna species diversity is still possible.

328 The most striking difference between the patterns in functional diversity (Fig. 1I-L) and
329 the other patterns is that the differences in functional diversity between current and
330 natural diversity are approximately equally evident both for all terrestrial species and
331 megafauna. This is at least partly a consequence of the highly size-selective nature of the
332 extinctions and range contractions affecting our size-based metric for functional
333 diversity. Though many patterns are different between natural and current distributions,
334 some constants emerge. One such constant pattern is the relative steepness of the gradient
335 between temperate and tropical regions of functional and species diversity. For both
336 current and natural diversity, the gradient is substantially shallower in functional diversity
337 than in the other diversity measures, corresponding to studies from other taxa (Mouillot *et*
338 *al*., 2014).

339

340 **(B) Geographic variation in diversity decifits**

The regional differences in faunal deficits are consistent with higher sensitivity of island regions and open areas to human pressures compared to continental forest regions. Only some of the island regions (Caribbean, Madagascar, and Australia) have large deficits among all terrestrial species, with Oceania having a much smaller deficit, similar to that of tropical Asia. The low deficits in Oceania could potentially be related to a higher survival in closed forest environments (Johnson, 2002) less accessible to humans, although it may be also partly a bias caused by poor knowledge of the Late Pleistocene mammalian fauna of many islands. The large deficits in the Greater Sahara (Fig. 2) and the desert regions of Australia (Figs. S6-S10), despite low human footprint in these regions (Wildlife Conservation Society, 2015), point to a higher sensitivity of arid faunas either directly via hunting or indirectly via anthropogenic environmental degradation. There is evidence for high prehistoric or historic hunting pressure in certain arid regions, such as the Middle East (Bar-Oz *et al*., 2011). Further, several species formerly inhabiting these regions were marginal populations that could be more sensitive to increased human pressures.

Anthropogenic diversity losses within a given time period may depend on losses during preceding periods. Africa experienced a large Early Pleistocene extinction, which was potentially caused by early *Homo* species (Werdelin & Lewis, 2013), and this has been suggested to be a contributing factor to the low loss of megafauna in Africa in the Late Pleistocene (Short & Smith, 1994). Similarly, the relatively low historic losses in the Americas may reflect that the massive prehistoric loss already had removed most sensitive species. Conversely, the lower prehistoric loss in South-East Asia and potential

363 survival of relatively sensitive species could explain its large historic losses and higher
364 fraction of threatened species compared to America (Sodhi *et al*., 2010). Our results
365 would thus be analogous to geographic patterns of threatened and extinct species
366 discussed for birds under Balmord's framework of extinction filters (1996).

367 Since we are only analyzing known species, we may underestimate the diversity loss in
368 poorly sampled places, e.g., tropical Asia. We note, however, that a recent detailed study
369 from India (one of the least sampled areas in tropical Asia) did not recover a single
370 extinct species in their sampling from five time periods spanning the last 200,000 years
371 (Roberts et al. 2014). The small tropical Asian megafauna extinction is therefore likely
372 real. We are more skeptical about tropical Australia where we suspect that the lack of
373 megafauna in the natural diversities could be a sampling artefact, although the small area
374 of region could also be a contributing factor.

375 We are convinced that the patterns we discuss are stable to the uncertainties in estimating
376 ranges based on indirect evidence such as climatic data and species co-occurrence
377 patterns. We do not focus on individual distributions, but only on combined diversities,
378 and the uncertainty in single-species distributions likely cancel each out. We use many
379 different assumptions for different species (Supplementary Data 1) and some researchers
380 could potentially disagree with some of these. We note, however, that out of the 226,825
381 additional cell occurrences in our analysis 25% are based on reported historic
382 distributions and 52% are the consequence of a fossil co-occurrence approach
383 (supplementary methods). The results will therefore likely be stable to any changes in the

384 remaining methods. The historical distributions can be considered fairly precise and
385 while the distributions based on fossil co-occurrences will be imprecise individually, the
386 approach produced diversity patterns very similar to the known historical (post-
387 Columbus) diversities when applied to extant large mammals in United States and
388 Canada (Table S11).

389 The patterns in phylogenetic diversity deficits are similar to those for species diversity,
390 although generally smaller (Fig. 2). This is most striking in Australia, which has suffered
391 substantially lower phylogenetic than species losses. A potential reason may be that
392 marsupials appear to have a higher evolutionary ecological plasticity than placental
393 mammals, so phylogenetic clades are less ecologically specialized and thus less
394 consistently sensitive to the same pressures. Exemplifying this, the two largest extinct
395 marsupial predators belongs to two different orders (Dasyuromorphia and Diprotodontia),
396 with the latter order also showing extremely large variation in body size(<10 g to >1 ton).
397 The cause of this large plasticity is unknown, but it could be a corollary of the more
398 limited scope for ecological specialization in marsupials caused by only having one set of
399 teeth (Werdelin, 1987) or the lower specialization potential in the marsupial skull
400 (Bennett & Goswani, 2013). Irrespective of the underlying cause, selective removal of
401 species based on ecological characteristics, such as body size, would remove a relatively
402 lower amount of phylogenetic history for marsupials than for placental mammals.

403

404 **(B) Biases in the inference in diversity drivers**

405 Our findings suggest that analyses of current patterns may cause a biased understanding
406 of the drivers of diversity. We find that mammalian diversity was more strongly linked to
407 vegetation productivity before being reshaped by human activities and that analyses of
408 current diversity patterns underestimate this relationship. This is likely a consequence of
409 the strong correlation between productivity and human population density (Evans &
410 Gaston, 2004). The differences in the importance of elevation range also suggest an
411 anthropogenic bias in the current patterns. All current diversities exhibited significant
412 positive correlations between diversity and elevation ranges, whereas this relationship
413 was non-significant for the natural diversity of megafauna and large species
414 diversity.Human accessibility may be highly correlated with elevation range as suggested
415 by a strong global correlation between elevation slope and remaining tree cover (Sandel
416 & Svenning, 2013) and by a higher elevation in new than in old records for re-discovered
417 presumed extinct mammals (Fisher 2011). Steep mountains may offer a refuge from
418 humans, both prehistorically (Johnson, 2002) and today (Gavashelishvili & Lukarevskiy,
419 2008). Therefore, our results suggest that the positive effect of elevation range on the
420 current diversity of terrestrial megafauna may be largely anthropogenic. On the other
421 hand, the still significant effect of elevational range for the natural diversity of all
422 terrestrial species (Tables S1-S3) suggests that elevation also has a non-anthropogenic
423 effect .

424 The performance of models of diversity drivers is often judged based on their explanatory
425 power (Jetz & Fine, 2012), and changes in R^2 values may change our understanding of
426 how well we understand diversity patterns. There is still substantial debate over the

causes of the overall diversity gradients (Brown, 2014). Part of the reason for this debate could be that the models are designed to explain natural diversity, but are applied to current diversity. The observed increases in pseudo-R^2 values when shifting to natural diversity suggest that we can explain diversity gradients better than we thoughtif we remove the human-induced biases. We use climatic data in estimating the range of some species (see supplementary materials and methods), which theoretically could create the pattern of increased pseudo-R^2 for the natural ranges (Fig. 3). For this to be a problem we would expect to see largest changes in the parameters annual precipitation and annual mean temperature, as these variables are used both in range estimation and in the diversity analyses. However, there was no such pattern for these predictors. The greatest changes are instead seen in NDVI, which was not used in any species' range estimation or for elevational range, where if anything NDVI should create a small bias opposite to what we observed (as we restricted the natural ranges of Caprinae to high elevation areas, which could have increased their natural megafauna diversity).

We have only focused on overall diversity patterns rather than clade- or region-specific patterns, but there is no reason to assume that the overall patterns are especially sensitive to human impact. Many studies have documented a strong human impact on smaller-scale distribution and diversity patterns (Laliberte & Ripple, 2004). Therefore, we suggest that researchers working on macroecological or macroevolutionary analyses of natural ecological and evolutionary drivers of diversity should focus on natural rather than current distributions whenever possible (maps of all distributions are available as

448 appendix 2-7, but the data can also be downloaded in a readily useable format at
449 http://bios.au.dk/om-instituttet/organisation/oekoinformatik-biodiversitet/data/).

450 The results of the present study illustrate the Anthropocene (Crutzen, 2002), a human-
451 dominated epoch in which few biological patterns and processes are not substantially
452 modified by humans (Helmus *et al*., 2014; Dirzo *et al*., 2014). Therefore, it is important
453 to integrate the potential effects of humans into any type of analysis. The estimated
454 natural distributions for all late Quaternary mammals will also be highly useful for
455 applied conservation projects and studies, enabling managers and researchers to use
456 present natural diversity as a baseline, e.g., for selecting species for rewilding projects or
457 reintroductions (Donlan *et al*., 2005; Hayward 2009).

458

459

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464 input from JCS. SF performed the analyses. SF and JCS wrote the paper.

465

466 **Data accessibility.**

467 The data reported in this paper are provided in the electronic supplementary material as

pdf files and in a readily useable format from http://bios.au.dk/om-instituttet/organisation/oekoinformatik-biodiversitet/data/.

Biosketches

Søren Faurby is a postdoc. He is an evolutionary biologist interested in the development, maintenance, and consequences of geographic variation within and between species, and he has investigated these subjects in a wide variety of taxa.

Jens-Christian Svenning is a professor. He is a broadly based ecologist, with core research interests including community and vegetation ecology, macroecology, biogeography, and physical geography. His work ranges from addressing basic ecological and evolutionary questions to investigating applied ecology, conservation biology, and global change.

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Supplementary Materials:

Supplementary Materials and Methods

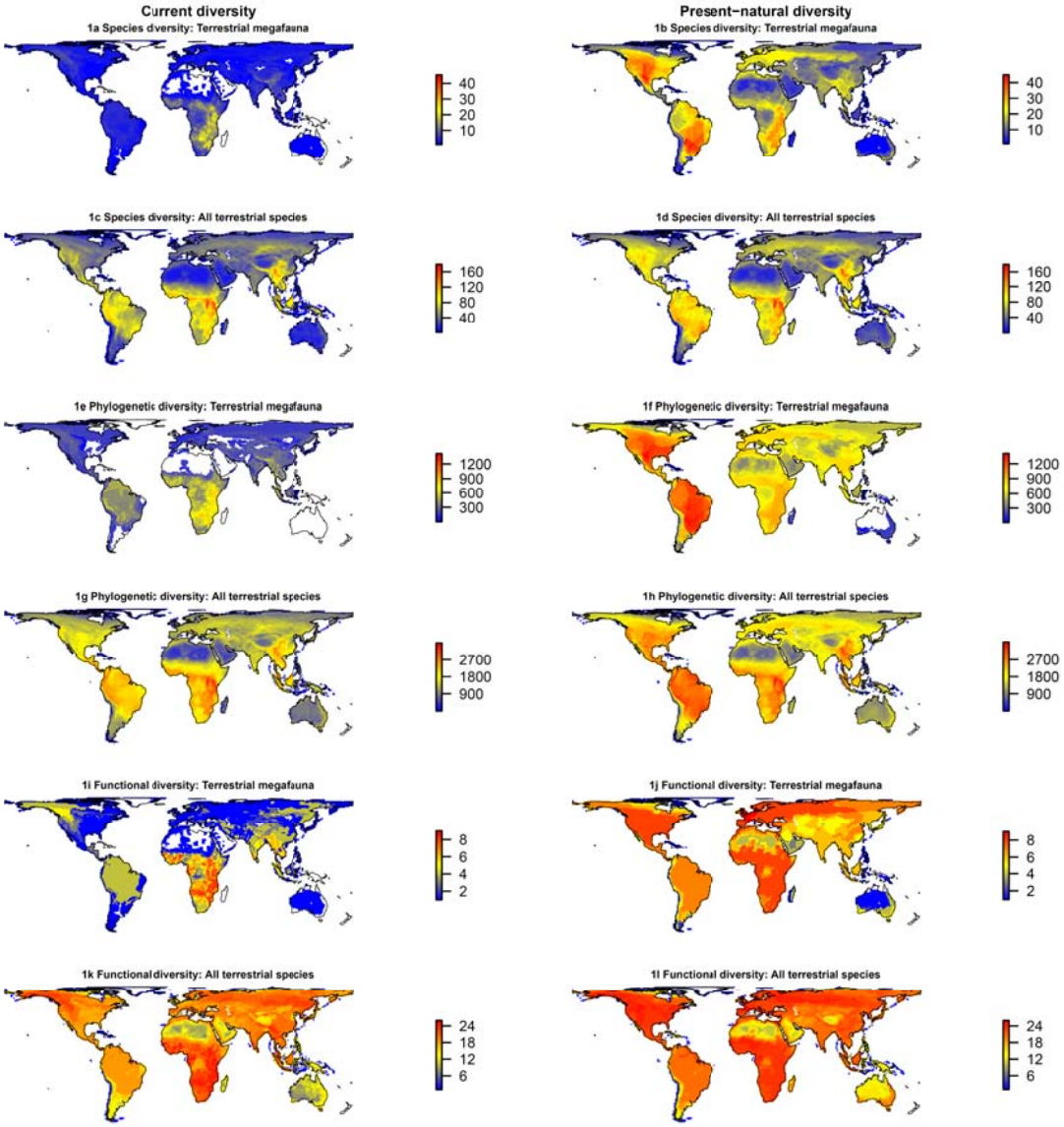
Supplementary Figures S1-S17

Supplementary Tables S1-S3

Supplementary Data 1-8

Figures

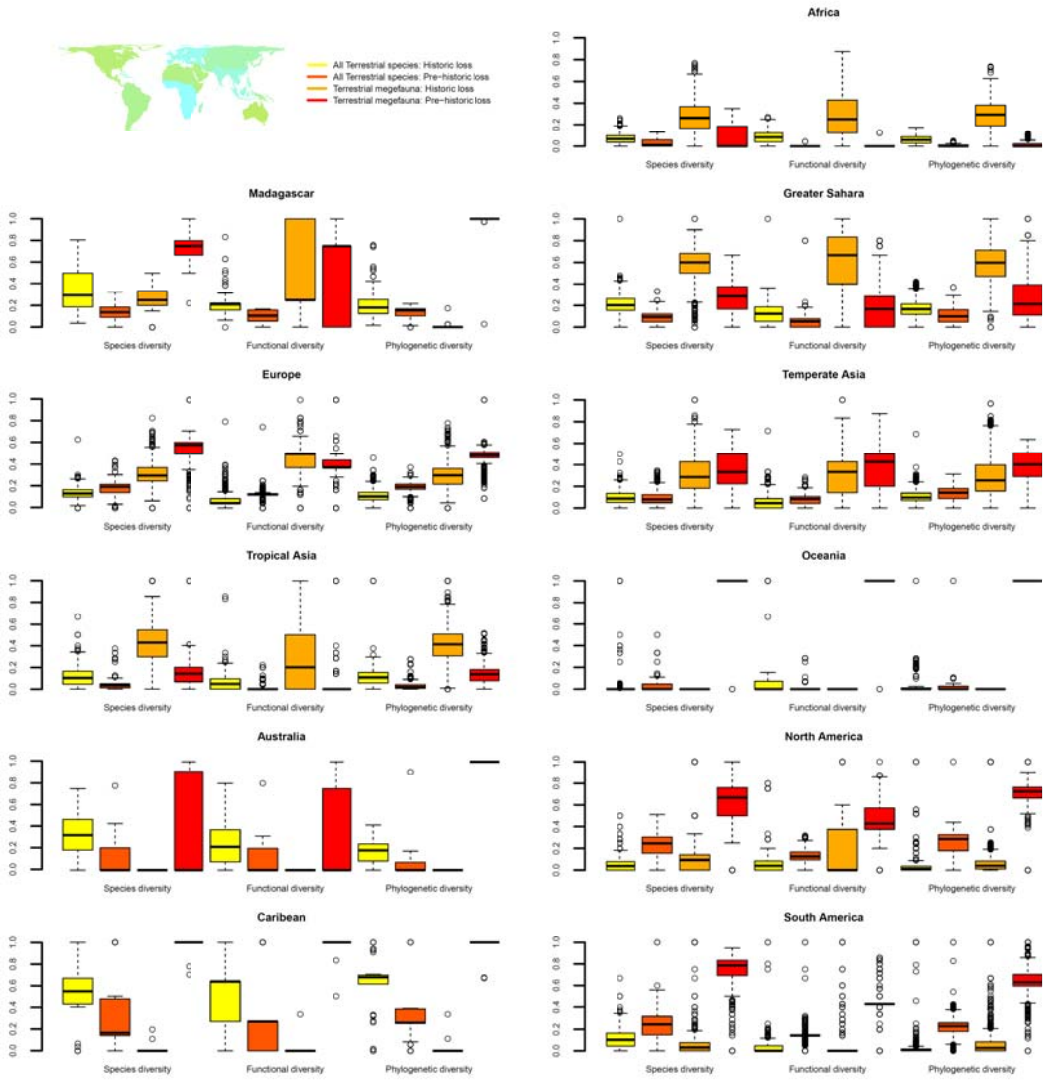
Figure 1



705

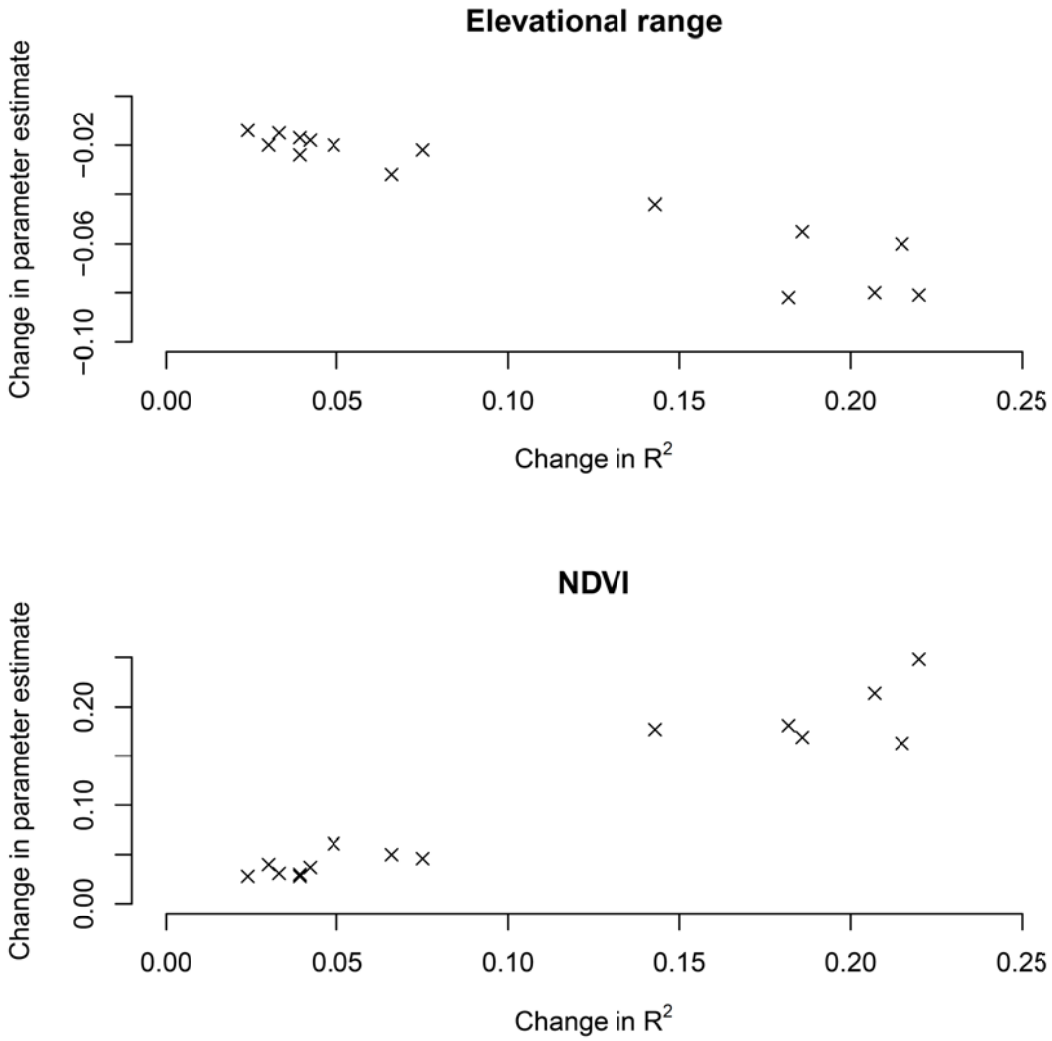
709 Current diversity and natural species, phylogenetic, and functional diversities for all
710 terrestrial mammal species and for terrestrial mammal megafauna (body size > 10 kg).
711 Colors are standardized horizontally so the same values in are given the same color in all
712 panels.

Figure 2



Estimated deficits in natural species, phylogenetic, and functional diversity for all terrestrial mammal species and terrestrial mammal megafauna species. The deficits are divided into those resulting from historic losses (the difference between current diversity and the present natural diversity of all species accepted by IUCN) and those resulting from prehistoric losses (the difference between the natural diversity for all species and for species accepted by IUCN). The thick middle line and box represent the median and first to third quartiles, respectively, and whiskers extend to the furthest datapoint that is no more than 1.5 times the interquartile range away from the median.

720 **Figure 3**



721

729 The x-axis shows the difference in pseudo-R^2 for the models of natural and current
730 mammal diversity (i.e., how much better the geographic pattern in natural diversities is
731 predicted by the full set of nine ecological predictors compared to the corresponding
732 current diversities using the same predictors). The y-axis shows the difference between
733 the standardized estimates of effect sizes of NDVI or elevation range for the natural
734 diversities compared to the corresponding natural diversities (i.e., how much stronger the
735 effect of elevational range or NDVI is for the former). The 15 crosses represent this
736 difference for each combination of one of the three diversities (species diversity,

729 phylogenetic diversity, functional diversity) and one of the five datasets (all species, non-
730 marine species, all terrestrial species, large terrestrial species, and terrestrial megafauna).
731 Plots of the one dimensional relationships between diversity and NDVI or elevational
732 ranges can be seen in figures S12-S17.